

NESTING BIOLOGY OF *OXYBELUS SERICEUS*
WITH A DISCUSSION OF NEST GUARDING BY MALE
SPHECID WASPS (HYMENOPTERA)

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INTRODUCTION

Among sphecid wasps males are regularly associated with nesting females only in a few species. A review of territorial behavior in male sphecids (Alcock, 1975) has shown that such behavior is typically associated with obtaining copulations. Only rarely do males actively participate in nest maintenance or prey manipulation. Species of *Oxybelus* digger wasps show an unusual diversity of male behavioral adaptations. Several species display male nest guarding behavior, that is, a male defends a territory at sites of active nests and attempts to mate with the nesting female (Peckham *et al.*, 1973; Peckham, 1977). Females exhibit an unusual prey carriage (impalement on the sting), and provision nests in exposed substrate with paralyzed Diptera.

Oxybelus sericeus is distributed throughout the United States and into Mexico (Bohart and Schlinger, 1957) and has been studied briefly by Bohart and Marsh (1960), who reported nest guarding. Here we present results of a two year study of the biology and behavior of *O. sericeus* in Georgia and discuss the phenomenon of nest guarding in sphecid wasps.

METHODS

Observations were conducted during 5 August to 15 September 1977 and 12 May to 12 June, 7 to 10 September, 7 to 9 October 1978 on St. Catherine's Island, 30 miles south of Savannah, Georgia at five separate study sites. Three beach sites were used primarily in 1977. The sparse dune vegetation consisted primarily of sandspur (*Cenchrus* sp.) navelwort (*Hydrocotyl bonariensis* Lam), and *Croton punctatus* Jacq. Air temperatures ranged between 32° and 40° C during May to

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September. In 1978 the Boiler site (see Fig. 5 in Matthews *et al.*, 1979) was mainly used. Observations were made from 0800 to 1800 on most days. Notes were taken in the field, supplemented with motion pictures of mating. Cell contents from nest excavations were transferred to sand-filled tins for rearing at room temperatures. Male observations used distinctively marked individuals and were mostly carried out at the Boiler site.

RESULTS

Activity Periods and Development. *Oxybelus sericeus* is a multi voltine species that first emerged in May and continued to nest into October. Rearing data revealed that both sexes required about 26 days (25 to 27 males, $n=7$; 26 to 27 females, $n=5$) to develop from hatched egg to an emerged adult. Males appeared first in the morning (0830 to 0930) about 15 to 30 minutes before females. After females ceased provisioning males dug sleeping burrows between 1700 to 1900, 2 to 3 cm deep in the nest area.

Nest Construction and Architecture. Nests were typically dug in exposed sand, but some females constructed nests under washed-up *Spartina* or shells. Nest structure is essentially the same as that of *O. subulatus* Robertson (Peckham *et al.*, 1973). The only difference was the absence of a tumulus about *O. subulatus* nests because of its carrier-type digging behavior. Nest digging in *O. sericeus* was initiated by biting the surface and pushing back the loosened sand with the legs. As the burrow deepened sand was apparently gathered between the venter and hind legs and pushed up the vertical burrow, forming a tumulus. Tumuli were leveled after digging was completed and ranged 2 to 5 cm in diameter. Leveling consisted of females repeatedly raking sand 1 to 3 cm away in all directions from the perimeter of the entrance, and returning to the entrance. In multicellular nests filler sand for the completed cell was obtained from the nest side burrow and cell excavation. Excess sand was brought to the surface, forming a tumulus which was subsequently leveled. After leveling, females began "orientation" flights, meandering paths 1 to 5 cm above the nest area, which lasted 2 to 5 min. and covered 1m^2 surrounding the nest.

Cell depths averaged 7.9 cm (3.5 to 15, $n=182$). Cell dimensions varied, averaging 16.8 mm (8 to 24, $n=97$) long and 5.6 mm (4 to 7, $n=99$) wide. An average of 1.7 cells was present per nest (range, 55%

had 1 cell and 0.9% had 6 cells). Final closure is similar to that reported for other *Oxybelus* (Peckham *et al.*, 1973) and this process took 35.5 min (15 to 45, $n=15$). Ten nests made by one female had from 1 to 6 cells per nest. Females often constructed series of nests in localized areas (ave. distance between 9 nests by 1 marked female was 10.9 cm, range 1.5 to 26 cm). One female was found nesting 400 m across salt marsh from its original nesting area. Intraspecific nest usurpation was observed once.

Provisioning and Prey Carriage. The mean duration between provisioning trips was 7.2 min. (1 to 140, $n=163$) with interruptions for mating included. Provisioning was most frequent between 1000 to 1700. Once a cell was full the female plugged the entrance from within the nest for oviposition and prey arrangement. Wasps provisioned up to three cells per day.

Ninety-six percent of the prey from 149 completed cells consisted of three species of Diptera (Table 1). Cells averaged 7 flies per cell (3 to 14, $n=152$); prey arrangement and egg placement may be classified as Crabro-style (Iwata, 1942).

Oxybelus sericeus females transported prey from salt marsh to the nest area using pedal type 1 carriage (Evans, 1962), using their legs to grasp the prey. Once alighted near the nest (5-100+ cm from the nest, termed the "initial landing site" in Peckham *et al.*, 1973) a female took a few seconds to face in the general nest direction. At this point she either impaled the prey on the sting (Fig. 1) or continued to carry the prey pedally as she crawled and/or flew the remaining distance to the nest. Some females only used pedal carriage as they transported prey entirely in flight, omitted the initial landing site and dropped into the open entrance (only very small flies were carried in this manner, see below).

Most *Oxybelus* transport prey from the point of capture to the nest area using pedal carriage (i.e. *bipunctatus* and *unighumis*, Peckham and Hook, in press). Prey is then impaled and the nest entered. *Oxybelus sericeus* differs from the others in that females may enter the nest using either pedal or impalement carriage. Our observations suggest that prey size influences the type of prey carriage used. Large, bulky prey normally elicited impalement carriage while small, less cumbersome prey were carried pedally. Prey weight corroborates this (Table 1). Ephydriids and some otitids averaged the least in weight and were rarely observed impaled, while dolichopodids averaged the heaviest and were usually impaled. Impalement carriage allows large

prey to be dragged, attached by the sting, enabling more efficient ground transport (the sting is impaled through a forecoxial corium, Steiner, 1979). Other factors may elicit impalement carriage. After copulation many females impaled (whether the prey was held pedally or impaled before copulation) and then entered their nests. Impaling under these conditions may speed up prey transport, minimizing further interruptions by males.

Mortality. Cleptoparasitic miltogrammine flies (Sarcophagidae) were regularly present at all sites, with the genera *Senotainia* and *Metopia* predominant. Miltogrammine maggots were found in 14.5% (n=75) of the cells excavated at the beach sites, but the Boiler site had only 3.7% (n=107). *Senotainia* flies were attracted to males, females and mating pairs. Flies often hovered or perched behind copulating pairs though larviposition was not observed. Most flies followed the male after separation, enabling the female to provision safely.

One beach site had 13.5% cell mortality due to the ant *Solenopsis pergandi* Forel (Formicidae). This ant appeared to rob cells while



Figure 1. A female *O. sericeus* with a fly (*Chaetopsis aenea*) impaled on her sting. Nest entrance is at left.

Table 1. Prey weights for most abundant prey captured by *Oxybelus sericeus* and a summary of 903 prey records from St. Catherine's Island, Georgia. Weights are from frozen and subsequently thawed prey and are presumably slightly less than fresh weight due to dehydration.

Species	Number recorded from all nests	%	Average weight (mg)	Range	Sample size
OTITIDAE					
<i>Chaetopsis apicalis</i> Johnson	209	21.3	0.34	0.13-0.59	103
<i>Chaetopsis aenea</i> (Wiedemann)	482	38.1	0.65	0.28-1.18	184
DOLICHOPODIDAE					
<i>Nanomyina litorea</i> Robinson	184	36.6	0.9	0.34-1.64	177
The remaining 4% of the prey consisted of:					
DOLICHOPODIDAE			EPHYDRIDAE		
<i>Paraclius</i> sp. (1)			<i>Notiphila bispinosa</i> Cresson (1)		
<i>Paraclius hybridus</i> Melander (2)			<i>Lipochaeta solossonae</i> Cresson (1)		
<i>Paraclius filifer</i> Aldrich (1)			<i>Polytrichophora conciliata</i> Cresson (1)		
<i>Thinophilis</i> sp. (1)			<i>Cirrula fuscifemur</i> (Steyskal) (7)		
<i>Thinophilis frontalis</i> Van Duzee (5)					
<i>Pelastoneurus</i> sp. (2)					
<i>Hypocharassus gladiator</i> Mik (4)					
<i>Hypocharassus pruinosis</i> (Wheeler) (2)					

tunneling below the surface. On three occasions, *Conomyrma* ants discovered active nests at the Boiler site and removed prey after recruitment of additional workers. *Conomyrma* ants were able to locate nests even after final closure. When excavating a completed nest, workers removed sand from the burrow until a stocked cell was reached. Mold accounted for 36% (n=33) cell mortality at the Boiler site (sometimes high tides covered this site).

Male Reproductive Strategies. Once a female began to nest, a male became closely associated with that nest as long as the female actively provisioned. Males perched near the entrance, either on the sand or a raised object (Fig. 2). Periodically the male changed positions, confining its activity to within 0.5 m of the nest. Guarding males often entered nests, particularly if females were late in returning, and sometimes stationed themselves head-out in the entrance, a guarding position typically used by *O. subulatus* (Peckham, 1977 and pers. obs.). Territories encompassed an area approximately 1 m in diameter surrounding the nest entrance. Males chased all



Figure 2. A guarding male of *O. sericeus* perched on a nest marker nail adjacent to an active nest.

intruding insects, especially rival males, and permitted only females to approach. Each time the female returned to or left the nest the guarding male attempted to mount. During copulation, the mounted male faced the same direction as the female, and used his middle legs to grasp the female's wings. The male's front legs were drawn in with the tarsi touching the female's pronotum and the hind legs helping to support her gaster (Fig. 3). During copulation males alternate between biting the female's vertex and cervical region and antennating her antennae or frons. Some males were observed to copulate over twenty times per day, with a gradual decline in the copulation duration from about 2 min. to about 10 sec.

After a female completed provisioning and plugged her entrance from within, the guarding male tended to patrol further from the nest, returning to inspect it intermittently. Such males usually took up defense of any unguarded nests they could locate. Presence of the male was not a prerequisite for provisioning; females nested whether or not a male guarded their nest.

Alternative to guarding of active nests we identified three other apparent male strategies: patrolling, guarding of the initial landing



Figure 3. Copulation in *O. sericeus*. The male is dorsal and grasps the female's wings with his middle legs while antennating her frons. The female's prey (*Nanomyia litorea*) has been temporarily dropped to permit copulation.

site and guarding lost prey. Patrolling consisted of cruising low (5 cm above ground) throughout the nest area without associating with particular nests. Males commonly used this behavior when searching for active nests to guard or exposed females. At times females provisioned infrequently, causing the majority of males to adopt the patrolling strategy. Guarding the initial landing site was possible because, as mentioned, prey-laden females typically land away from the nest and then proceed to enter. On five occasions a male ceased nest guarding and instead took up defense of a territory about the initial landing site. Two conditions seemed prerequisite to this strategy: first, intense male competition for the nest territory; second, a propensity by the female to land repeatedly in the same area prior to entry. On ten occasions prey were abandoned by females when intensively interfered with by one or more males. When this occurred, males perched next to the prey, chased off intruding males and copulated with the female if she returned.

Male-Male Competition. It became apparent during the 1977 season that there was considerable individual variation in the number

of copulations obtained and that individual males were not limited to a single mating strategy. At the Boiler site we followed interactions between marked individuals daily for 22 days (15 May to 5 June). Of 51 males marked, 13 were observed an average of 7.5 days (5 to 13), 29 for 1 to 3 days and 9 were marked the last three days of the study. In addition to clarifying male mating strategies these data revealed that individual males differed greatly in their success in acquiring and defending nest territories.

Usually 5 to 12 males actively competed for territories and matings each day. Though the composition of males changed daily as new wasps emerged and marked ones disappeared, three males dominated our data. These "dominant" males won most encounters and thus were rarely forced to abandon a nest territory when challenged. Moreover, the "dominant" males quickly abandoned inactive nests and patrolled until they located an unguarded or (more likely) a guarded nest. Violent, aggressive interactions (Fig. 4) occurred between nearly equal size males competing for the same nest. An intruding male flew directly at the guard, and a fierce grappling match resulted, lasting from several seconds to over one minute. Often a series of grappling matches took place before one male retreated. "Dominant" males frequently usurped nest territories from other guarding males; one male usurped 15 territories in four days. Females displayed no obvious behavioral change when new males took over their nest territory. We believe that the isolation and relatively small size of the Boiler site area (7.6×2.4 m) enabled individual males to establish and maintain their dominance. One male won all encounters over a seven-day period and another male was completely dominant over a different four-day period.

Female Receptivity. Upon eclosion females were sexually receptive, allowing males to copulate for 2 to 3 minutes ($\bar{x}=2.5$, $n=4$), after which males dismounted. When mounted a female submitted quickly by raising her gaster, allowing copulation. Newly emerged females required a few days to develop mature eggs (dissections of newly eclosed wasps revealed small, clear eggs beginning to develop in the ovarioles). These females spent considerable time investigating the nesting area and were therefore easy targets for patrolling males.

Once nesting began, females tended to avoid males when digging or provisioning. When intercepted, females varied in their response; some allowed a male to mate on most trips to the nest without



Figure 4. A pair of *O. sericeus* males grappling to determine territory ownership.

struggling, while others more strongly resisted male advances. Resistance consisted of bending the gaster down and pygidium forwards, or dragging the mounted male and prey towards the entrance. Females appeared to initiate the termination of copulation by struggling, thereby inducing the male to dismount, although persistent males at times ignored such signals.

Provisioning females mainly interacted with guarding males, but sometimes they were mounted by as many as four different males between the initial landing site and their burrow. Rarely a female dragged a mounted male and prey to the nest entrance, and squeezed past him into the burrow without permitting copulation. More commonly, male and prey were too cumbersome to transport (especially if over 50 cm from the nest); in this situation prey-laden females more readily submitted.

DISCUSSION

The most efficient strategy for *O. sericeus* females appears to be to allow males to copulate, thereby minimizing the total energy and time spent in the interaction. The size of the nest area, density of nests, and the operational sex ratio probably greatly influence the quantity and intensity of male-female interactions. In order to better understand possible selective forces acting to bring about nest guarding in *Oxybelus*, comparison will be made with other nest guarding sphecids (Table 2). Wasps that have males associated with the parental nest (e.g. *Microstigmus*, *Philanthus* and *Cerceris*) are excluded here, but twig, cavity and mud nesters are included in Table 2 mainly to suggest that such interesting wasps deserve further study.

Males in some species cue in on provisioning females. These males patrol and also perch next to active nests, though not associating with any particular nest. For this to evolve requires that females remain receptive throughout the nesting cycle. For a male the advantage would be in the increased probability of his sperm fertilizing the egg, assuming sperm precedence which is well documented in other insects (see Lefevre and Jonsson, 1962; Boorman and Parker, 1976; Smith, 1979). Gillaspay (1962) found males of *Sphex trepanecus* Saussure to cue in on provisioning females. When a prey-laden female approached her nest a male would appear and copulation occurred near the nest. The crabronine genus *Lindenius* commonly has males searching and entering nest entrances and Miller and Kurczewski (1973) hypothesized that such "nest searching" behavior may help reduce cleptoparasitism (by miltogrammine flies and chrysidid wasps) in dense aggregations. *Oxybelus emarginatus* normally has males patrolling nest areas but Krombein (1964) once found males in Florida not only patrolling and perching but also mounting and copulating with provisioning females. One of us (AWH) recently briefly observed the same behavior in *O. emarginatus* near Mission, Texas, only no copulations were observed. This ability to cue in on provisioning females probably developed early in the evolution of nest guarding.

The transition from the ability to intercept provisioning females to establishment of territories in the nesting area seems a logical step. In *Sphex cognatus* Smith (Ribi and Ribi, 1980) and *Tachysphex* species (Kurczewski, 1966) males are known to maintain territorial stations in nesting areas and copulate with nesting females. In several other species male territories always include at least one female nest. These

include *Oxybelus subulatus* (Peckham, 1977), *Stizus* (*Megastizus*) *texanus* Cresson (Gillaspy, unpubl.) and *Tachytes distinctus* Smith (Lin, 1963; Lin and Michener, 1972). *Stizus texanus* nested near Matamoros, Mexico and males defended nest territories, copulating with provisioning females. *Tachytes distinctus* defended nest territories but did not attempt to mate with provisioning females. Research on *Trypargilum* suggests that male guarding helps reduce cleptoparasitism and supersedure by other wasps and bees (Krombein, 1980). Males may also assist in nesting activities and females of at least one species will not provision unless a guard is present (Coville and Coville, 1980).

Peckham (1977) provides quantitative data on the effect of male *O. subulatus* in reducing miltogrammine cleptoparasitism. Unguarded nests had 33% (examined 85 cells) cleptoparasitism while guarded nests had only 18% (n=84). "Thus the presence of the male appears to have significantly reduced miltogrammine cleptoparasitism." The low rate of cleptoparasitism in *O. sericeus* at the Boiler site can be taken as indirect evidence that guards in this species reduce cleptoparasitism.

Earlier stages in the evolution of nest guarding as found in *Oxybelus sericeus* may be found in other *Oxybelus*. Several *Oxybelus* (*bipunctatus*, *subcornutus* Cockerell, *emarginatus*, Peckham *et al.*, 1973 and pers. obs.; *decorosus*, *uniglumis*, Peckham and Hook, in press) fit this pattern whereby males patrol the nest area, indiscriminantly chasing nearby moving insects. Peckham *et al.* (1973) found only 6% fly cleptoparasitism in an aggregation of *O. bipunctatus*, and attributed this low figure partially to male harassment of miltogrammine flies.

In summary, we suggest the following scenerio for the evolution of nest guarding in sphecid wasps. Initially males cue in on females who are actively provisioning nests and who remain continuously receptive to copulation attempts. Under certain ecological conditions the benefits resulting from defense of an area (territory) within a nest aggregation will exceed the costs to males. Sperm precedence may be an important factor in this context, if it occurs, for the last male to inseminate a female prior to oviposition will have increased fitness relative to other males. An incidental but important effect of the male's presence and activity is to reduce levels of cleptoparasitism (and perhaps supercedure) thereby improving a female's nesting success relative to females inseminated by non-territorial males. It

Table 2. A compilation of records of male involvement in nesting in sphecid wasps arranged systematically following Bohart and Menke (1976).

Subfamily, tribe	Species	♂ associates to mate w/ w/individual ♀ at or near nest	♂ attempts ♂ deters clepto- parasites	♂ assists in nesting activities	Source
Sphaginae					
Sceliphronini	<i>Dynatus nigripes</i>	yes	—	no	Kimsey, 1978
	<i>Trigonopsis cameronii</i>	yes	yes	no	Eberhard, 1974
Sphecini	<i>Sphex trepanecus</i>	?	—	no	Gillaspy, 1962
	<i>Sphex cognatus</i>	no	—	no	Ribi & Ribi, 1979
Pemphredoninae					
Pemphredonini	<i>Diodontus virginianus</i>	no	—	no	Krombein, 1958
Larinae					
Larini	<i>Tachytes distinctus</i>	yes	—	no	Lin, 1963; Lin and Michener, 1972
	<i>Tachytes auricomans</i>	no?	—	no	Hook, unpublished
	<i>Tachysphex apicalis</i>	no	—	no	Kurczewski, 1966
Trypoxylonini	<i>Pison strandi</i>	yes	—	—	Masuda, 1939; Tsuneki, 1970
	<i>Trypoxylon fabricator</i>	yes	—	—	Rau, 1933
	<i>Trypargilum collinum</i>	yes	yes	yes	Peckham & Peckham, 1898; Paetzl, 1973; Krombein, 1967
	<i>Trypargilum striatum</i>	yes	—	—	Peckham & Peckham, 1898; Rau, 1928; Krombein, 1967

Subfamily, tribe	Species	♂ associates w/individual nest	♂ attempts to mate w/ ♀ at or near nest	♂ deters clepto- parasites	♂ assists in nesting activities	Source
	<i>Trypargilum texense</i>	yes	—	—	—	Hartman, 1905
	<i>Trypargilum clavatum</i>	yes	yes	—	yes	Rau, 1928; Krombein, 1967
	<i>Trypargilum politum</i>	yes	yes	—	yes	Rau, 1928; Fattig, 1936
	<i>Trypargilum spinosum</i>	yes	—	—	—	Lin, 1979
	<i>Trypargilum orizabense</i>	yes	—	—	—	Coville, 1979
	<i>Trypargilum tridentatum</i>	yes	—	—	—	Krombein, 1967
	<i>Trypargilum tenocitlan</i>	yes	yes	yes?	yes?	Coville & Coville, 1980
Crabroninae						
Oxybelini	<i>Oxybelus subulatus</i>	yes	yes	yes	no	Peckham <i>et al.</i> , 1973; Peckham, 1977
	<i>Oxybelus sericeus</i>	yes	yes	yes	no	Bohart & Marsh, 1960; Hook & Matthews, this paper
	<i>Oxybelus emarginatus</i>	no	yes	—	no	Krombein, 1964; Hook, pers. obser.
Crabronini	<i>Lindenius panzeri</i>	no	yes	—	no	Minkiewicz, 1934
	<i>Lindenius columbianus</i>	no	yes	yes	no	Miller & Kurczewski, 1973
	<i>Lindenius armaticeps</i>	no	yes	yes	no	Ibid
	<i>Lindenius buccandentis</i>	no	yes	yes	no	Ibid
Nyssoninae						
Stizini	<i>Stizus megastizus</i>					
	<i>texanus</i>	yes	yes	—	no	Gillaspy, unpublished

would be further enhanced if males focused their territorial activity around active nests. If females exercise a preference for presence of a guarding male prior to initiating nesting (e.g. *Trypargilum*), then this behavior would spread in the population, since it would directly benefit the interests of both sexes. The possibility exists that males could ultimately be induced to guard nests without requiring repeated matings as is reported for *Tachytes distinctus* (Lin, 1963; Lin and Michener, 1972). However, such cases are in need of further study. In digger wasps, delays in provisioning and exposure to predators and cleptoparasites constitute important risks for females; but rejection of males may be costly in terms of time, energy and loss of resource (the nest). Such costs to the female must be important, otherwise females of *O. sericeus* would not often attempt to sneak past guarding males when provisioning. Guarding males also incur real costs in addition to time and energy expenses. Gwynne and O'Neill (1980) recently showed that territoriality in *Philanthus* males resulted in increased mortality due to sex-biased predation. In *Oxybelus sericeus* the balance struck appears to effect a significant reduction in levels of cleptoparasitism, so male guarding directly benefits the interests of both sexes.

SUMMARY

The multivoltine wasp *Oxybelus sericeus* nested continually from early May to October on St. Catherine's Island, Georgia. Nest sites were situated in sand just above a tidal salt marsh where the females hunted prey. Two otitid flies, *Chaetopsis apicalis* and *C. aenea* and one dolichopodid, *Nanomyia litorea*, comprised 96% of the prey. Up to three cells per day were stocked with an average of 7 (range 3 to 14) flies per cell. Prey were transported pedally from point of capture to the nest area whereupon females either continued pedal transport or impaled the fly on the sting before continuing to the nest. Number of cells per nest averaged 1.7 (range 1 to 6) with individual females varying the number of cells in successive nests. Cell depths averaged 7.9 cm (range 3.5 to 15). Males were active in the nest area and utilized five different mating strategies. Patrolling and nest guarding were the most common strategies. Certain individuals were found to dominate all other males in encounters in a small nesting area. These dominant males shifted their guarding activities to "track" actively nesting females for up to seven days. Miltogrammine fly parasitism ranged

from 3.7% to 14.5%; *Senotainia* sp. was the predominant parasite, but *Metopia* sp. was also recorded. Ants (*Solenopsis pergandei* Forel and *Conomyrma* sp.) were nest predators, with 13.5% cell mortality due to *Solenopsis* recorded at one site. Records of male association with nesting females are summarized from the literature. The idea is developed that the effect of a male's presence and activity in reducing mortality from cleptoparasitism supersedure has been an important factor in the evolution of male nest guarding and female's toleration of interference due to repeated copulation attempts.

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